Hawai'i Coral Reef Assessment and Monitoring Program: Spatial Patterns and Temporal Dynamics in Reef Coral Communities[1]

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Abstract: The Hawai'i Coral Reef Assessment and Monitoring Program (CRAMP) was established to describe the spatial and temporal variation in Hawaiian coral reef communities in relation to natural and anthropogenic factors. Sixty permanent reef sites stratified by depth have been monitored in the main Hawaiian Islands since 1999 and formed the basis for analysis of temporal change over the initial 3-yr period. A rapid assessment technique (RAT) was developed to supplement the monitoring site data and provide much wider geographic coverage, but with a focus on spatial patterns rather than temporal change. Analysis of these data supports and amplifies the results of many other ecological studies on Hawaiian reefs. The data revealed that the major natural factors influencing reef coral community structure in Hawai'i include depth, wave height, wave direction, island age, rugosity, and sediment grain size. Possible anthropogenic influences and trends also appeared in the data. Areas of decline appear to be concentrated on islands with high human population or in areas suffering from extensive sedimentation. Reefs receiving high terrigenous runoff contain sediments with high organic content. Spatial analysis showed an inverse relationship between percentage organics and coral species richness and diversity. Reef coral communities can undergo natural oscillations over a period of years, so continuation of the CRAMP longer-term monitoring is required to establish long-term (decadal) environmental trends.

Until recently, coral reef studies in Hawai'i were largely conducted over small spatial and temporal scales to address highly localized issues. There was little uniformity in methodology, so inference about large-scale and long-term ecological processes and patterns was lacking. Hughes and Connell (1999) pointed out that studies of one reef or a few reef sites over a short period of time can be misleading and a longer-term approach over a wide spatial range is needed. In response to this research need, the Hawai'i Coral Reef Assessment and Monitoring Program (CRAMP) was developed in 1998.

Environmental variables such as wave exposure and habitat complexity have been shown to strongly influence reef fish assemblage characteristics on a large spatial scale (Friedlander et al. 2003). It has been noted that wave energy is one of the primary forcing functions on benthic communities in Hawai'i (Dollar 1982, Grigg 1983). In addition, impact of other environmental parameters such as habitat complexity, sediment composition, adjacent watershed characteristics, and anthropogenic factors on the coral reef benthos have not been explored at a statewide scale (Friedlander et al. 2003). This paper

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focuses on the results of initial studies of the spatial and temporal trends in coral communities around Hawai'i and evaluates the relationship between coral assemblages and some of the natural and anthropogenic factors that shape them. The results of this work serve as a benchmark for future monitoring of coral communities in Hawai'i as part of the National Action Plan (U.S. Coral Reef Task Force 2000).

MATERIALS AND METHODS

Pilot studies were conducted before the initiation of the monitoring program to develop an appropriate method that could detect absolute change in coral cover over a wide range of hard-bottom habitats with high statistical power (Brown et al. 2004 [this issue]). CRAMP monitoring sites were selected on the basis of existing data, accessibility, degree of perceived environmental degradation by expert observers, level of management protection, and extent of wave exposure. Two reef areas, a shallow (generally 3 m) and a deep (generally 10 m) station, were surveyed at each of the 30 statewide locations. Each station was established with 10 randomly chosen 10-m permanent transects on hard bottom marked by small stainless-steel stakes at the endpoints. Digital video, fixed photoquadrats, visual belt fish transects (Brock 1954), substrate rugosity, sediment samples, and other qualitative data were collected at various times over the study period. Digital video imagery was taken perpendicular to the substrate along each transect at a height of 0.5 m. Twenty randomly selected, nonoverlapping digital video frames from each transect were used to estimate benthic coverage. PointCount99 software was used to tabulate coral and benthic substrate types at each of 50 randomly selected points per image and generate percentage coverage data (http://www.cofc.edu/~coral/pc99/PC99manual.htm). Total mean percentage coral cover by station, mean percentage coral cover by species within a station, species richness (number of species per transect), and diversity were used as dependent variables in this study. Coral diversity was calculated using the modified Shannon-Weaver diversity index (Loya 1972). Each of the 60 stations was surveyed at least twice over the last 4-yr period (Figure 1). Constraints on resources and adverse weather and surf conditions prevented sampling of each station every year.

Analysis of the initial monitoring data (Friedlander et al. in press) indicated that a much larger spatial array of sites was desirable because the coral reefs of Hawai'i are diverse and show high variability for many ecological parameters. Thus, the monitoring site data were supplemented in the spatial dimension using a rapid assessment technique (RAT). The RAT is an abbreviated version of the CRAMP monitoring protocol, using a single 10-m transect to describe benthic cover, rugosity, and sediments. This protocol generates the same biological data (i.e., percentage cover, species richness, and diversity) and environmental data (e.g., rugosity, depth, sediments, etc.) as the CRAMP monitoring data set. Multiple RAT transects were chosen randomly using ArcView spatial analyst (Environmental Systems Research Institute 1998). These transects were stratified on hard-substrate habitats in a manner similar to that used at the CRAMP monitoring sites but along a full range of depths (Figure 1). The advantage of the RAT is that it allows for the very rapid acquisition of data suitable to describe the variation in communities and the forces controlling these distributions in a spatial framework. The RAT is not designed to produce the type of data needed to detect temporal change. Such data are gathered at the 60 CRAMP monitoring stations.

Rugosity was measured using the chain and tape method (McCormick 1994). A light brass chain marked off in 1-m intervals was spooled out over the bottom along the entire length of each 10-m CRAMP transect. The amount of chain necessary to span the distance between the two marker pins was divided by the straight-line tape measurement to generate an index of rugosity for that transect.

Two sediment samples (approximately 500 cm^3 each) were collected haphazardly within each study area and mixed to assure homogeneity of each sample. This mixture was di-

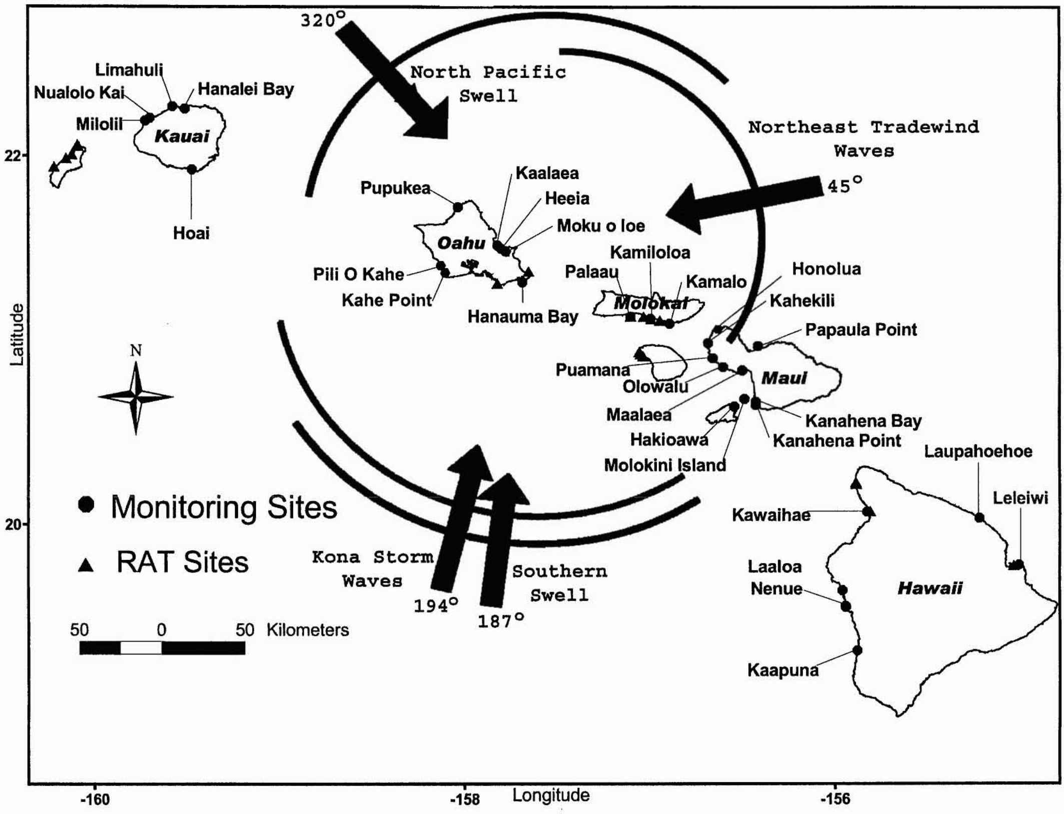

FIGURE 1. Map of the main Hawaiian Islands showing the 30 monitoring sites (labeled by name) and the clusters for the 92 rapid assessment (RAT) sites. At each monitoring site there are two stations, one in shallow water (generally 3 m) and one in deep water (generally 10 m). General direction of waves influencing the Hawaiian Islands (arrows) are also shown for reference (after Moberly and Chamberlain 1964).

vided into four subsamples. Standard brass sieves with opening diameters of 2.8 mm, 500 µm, 250 µm, and 63 µm and a brass catch pan were used to provide four sediment size fractions: medium sand, fine sand, very fine sand, and silt, respectively. Two of the sediment subsamples were wet sieved through the stacked sieves. All washings were collected and filtered to determine the silt fraction. The sediment fraction remaining on each sieve was washed through preweighed filter paper (Whatman Brand 114 wet-strength, 25 µm) and air-dried to constant weight. The percentage weight of each grain size was determined by calculating the ratio of the various size fractions to the total sample weight. Approximately 30 g of material from the other two subsamples was air-dried to a constant weight. From each, 10 g was ground with mortar and pestle to a fine, homogeneous material and placed in preweighed crucibles. These were placed in a drying oven at 100°C for 10 hr, cooled in a desiccator, and weighed. Next, the crucibles were placed in a muffle furnace at a temperature of 500°C for 12 hr, cooled in a desiccator, and reweighed. Weight loss at 500°C was assumed to be due to burning off of the organic fraction (Craft et al. 1991). This analysis may overestimate absolute percentage values of organic material, so only relative differences were compared among sites for this parameter.

Other ancillary variables included the following: (1) total human population within

5 km of each site was calculated using 2000 census data from the State of Hawai'i Geographic Information System (GIS) (http://www.state.hi.us/dbedt/gis/); (2) mean annual rainfall (mm), total area of the adjacent watershed, and population within the watershed was obtained for each site from the State of Hawai'i GIS web site; (3) mean, minimum, and maximum values for offshore significant wave height (m) along with wave direction (compass bearing) were downloaded daily from the Naval Oceanographic WAM model web site (http://www.navo.navy.mil) for 2001; (4) geologic age of the volcano underlying each site was estimated using data from Clague and Dalrymple (1994); (5) management status rank was included as a categorical predictor and pooled into three categories. A rank of 3 was assigned to Marine Protected Areas (MPAs) with the highest degree of protection (generally "no take" areas). Rank 2 included sites with a moderate degree of protection such as restriction of certain fishing techniques such as gillnetting and/or spearing or areas closed to taking of certain species. Rank 1 consisted of open access areas.

For statistical analysis, selective variables were transformed to meet the assumptions of normality. These variables were then normalized and placed on a common dimensionless measurement scale for subsequent spatial analysis (Clarke and Warwick 2001). Percentage data were arcsin–square root transformed, and other heteroscedastic data were transformed using log $(x + 1)$. Individual RAT transects ($n = 92$) were run using only the first 10-m CRAMP transect at each of the monitoring stations ($n = 60$) to allow for comparisons on the same measurement spatial scale (transect area 3.5 m^2). Statistical analysis of these data was conducted using Statistica 6.0 (StatSoft 2001) and PRIMER 5.0 (Clarke and Gorley 2001) software to examine both univariate and multivariate aspects of the spatial data sets.

A General Linear Model (GLM) was conducted with total coral cover as the dependent variable regressed against the continuous predictors: rugosity, depth, percentage organics, percentage grain sizes, wave parameters, human population parameters, precipitation, watershed area, and geologic age of the site. Management status rank was included in the model as a categorical predictor. A Best Subset routine was performed using Mallows C_p as the selection criteria to generate an appropriate first-order model. Before the regression analysis all explanatory variables were analyzed for collinearity. Selected variables from the paired comparison, which exhibited a correlation >0.9, were removed from the analysis. This is somewhat conservative because Clarke and Warwick (2001) recommended the reduction of data subsets with mutual correlations >0.95. Separate GLM analyses were also performed using the Best Subset routines with coral species richness and diversity regressed against the previously mentioned independent variables.

Multivariate analysis was performed using correspondence analysis (CA). Percentage coral cover of the six most abundant species was examined using CA for the spatial data. In addition, patterns in coral cover by species were examined in relation to environmental variables using the BIOENV procedure in PRIMER. This procedure compares dissimilarities between a biotic data matrix (percentage cover for dominant coral species by samples) and an abiotic data matrix (environmental variables by samples) to maximize rank correlations and produce the best environmental variable combinations that explain the variation in the biological data (Clarke and Warwick 2001). The environmental variables for each site were the same as listed in the univariate section.

Temporal trends were analyzed using Statistica 6.0 software. Data from each monitoring station were analyzed separately due to differences in sampling intervals and sample size. Percentage coral cover values were arcsin–square root transformed to produce a data set with homogeneous variances and an underlying distribution that was approximately normal. A repeated-measures analysis of variance test within the GLM procedure was used for each station. Contrasts were then used to test for differences between mean percentage coral cover from the initial baseline survey to the most recent survey conducted at a station. Due to the unbalanced design each station was tested separately and therefore no multiple pair-wise comparisons were used. A GLM procedure was then used to test for differences in percentage change in coral cover among the following continuous predictors: initial coral cover, rugosity, depth, percentage organics, percentage grain sizes, wave parameters, human population parameters, precipitation, management rank, watershed area, and geologic age of the site. Raw values for percentage change were used in the analysis due to the moderate normality of the data set, relative homoscedasticity, and the presence of negative values (Zar 1999).

RESULTS

Coral coverage measured at each site between 1999 and 2002 is shown in Table 1. Average coral coverage for all 152 reef stations combined was 20.8% $\pm$ 1.7 SE, with six species accounting for most of the coverage (20.3%). The six dominant species were as follows: *Porites lobata* (6.1%), *Porites compressa* (4.5%), *Montipora capitata* (3.9%), *Montipora patula* (2.7%), *Montipora flabellata* (0.7%), and *Pocillopora meandrina* (2.4%).

Spatial Patterns

The univariate Best Subset regression model for total coral cover was significant ($R_a^2 = 0.46$; $F = 22.1$; df $= 6{,}145$; $P < 0.001$) among stations. Variation in coral cover was best explained by rugosity ($F = 97.8$; df $=$ 1,145; $P < 0.001$), depth ($F = 4.4$; df $=$ 1,145; $P = 0.037$), percentage fine sand ($F = 8.5$; df $=$ 1,145; $P = 0.004$), mean wave direction ($F = 9.92$; df $=$ 1,145; $P = 0.002$), rainfall ($F = 4.1$; df $=$ 1,145; $P = 0.044$), and geologic age ($F = 5.3$; df $=$ 1,145; $P = 0.023$) (Table 2). The Best Subset first-order model indicated that a positive relationship existed between coral cover and rugosity, depth, and percentage fine sand. Coral cover had a negative relationship with mean wave direction, rainfall, and geologic age.

Variation in coral species richness ($R_a^2 = 0.20$; $F = 8.8$; df $= 5{,}146$; $P < 0.001$) was best explained by rugosity ($F = 8.1$; df $=$ 1,146; $P = 0.005$), percentage organics ($F = 12.9$; df $=$ 1,146; $P < 0.001$), mean wave direction ($F = 20.8$; df $=$ 1,146; $P < 0.001$), and geologic age ($F = 7.6$; df $=$ 1,146; $P = 0.007$) (Table 2). Population within 5 km also appeared in the model but was marginally nonsignificant ($F = 2.4$; df $=$ 1,146; $P = 0.12$). The Best Subset first-order model indicated that a negative relationship existed between coral species richness and all of these parameters except rugosity.

Coral diversity ($R_a^2 = 0.21$; $F = 6.7$; df $=$ 7,144; $P < 0.001$) variation was explained by rugosity ($F = 4.9$; df $=$ 1,144; $P = 0.028$), percentage organics ($F = 18.7$; df $=$ 1,144; $P < 0.001$), percentage medium sand ($F = 8.0$; df $=$ 1,144; $P = 0.005$), mean wave height ($F = 5.9$; df $=$ 1,144; $P = 0.016$), mean wave direction ($F = 20.0$; df $=$ 1,144; $P < 0.001$), and geologic age ($F = 6.7$; df $=$ 1,44; $P = 0.010$) (Table 2). Percentage fine sand ($F = 3.4$; df $=$ 1,144; $P = 0.067$) also appeared in the model but did not explain a significant portion of the variation. A negative relationship was found between diversity and percentage organics, percentage medium sand, percentage fine sand, mean wave direction, and geologic age. Rugosity and mean wave height had a positive relationship on coral diversity.

Multivariate correspondence analysis (CA) testing coral cover by species showed a tight linear cluster of sites with a small number of sites scattering along a second axis (Figure 2). Dimension 1 and dimension 2 accounted for 56% of the total variation in the data. Sites in the upper left quadarant of Figure 2 were dominated by the branching coral *Porites compressa*. These *P. compressa* communities typically included an abundant component of the coral *Montipora capitata* and were found in low-wave-energy environments in deeper waters or in sheltered bays. The end-member communities graded into moderate-wave-energy sites characterized by the massive coral *Porites lobata* along the middle portion of the linear cluster. The sites in the upper right-hand quadrant were shallow areas experiencing high wave energy and dominated by the branching coral *Pocillopora meandrina*.

TABLE 1

Change in Percentage Coral Cover over Time at Each Station

Island	Station	Depth (m)	1999	2000	2001	2002	Increase	Decrease[a]	P^b
Kaua‘i	Hanalei	3	16.1	25.6		17.0	0.9		0.65
	Hanalei	8	28.1	30.3		26.0		−2.1	0.99
	Ho‘ai Bay	3	10.8		10.8	11.4	0.7		0.37
	Ho‘ai Bay	10	3.2		6.3	5.7	2.4		**0.006**
	Limahuli	1	14.9	14.5		22.8	7.9		**0.006**
	Limahuli	10	19.5	20.3		25.1	5.5		**0.007**
	Miloli‘i	3	3.7	5.7		4.1	0.4		0.46
	Miloli‘i	10	14.1	13.2		16.4	2.4		0.07
	Nu‘alolo Kai	3	2.8	4.6		3.6	0.7		0.06
	Nu‘alolo Kai	10	20.7	24.1		20.2		−0.5	0.79
O‘ahu	Hanauma Bay	3	23.6	25.8		21.8		−1.8	0.50
	Hanauma Bay	10	26.7	27.0		22.2		−4.5	**0.04**
	He‘eia	2	36.3	22.7	18.0	24.2		**−12.1**	**0.003**
	He‘eia	8	7.8	7.5	7.0	4.7		−3.1	**0.01**
	Kahe Pt.	3	11.9		15.0	15.1	3.2		**0.004**
	Ka‘alaea	2	62.2	50.7	49.1	67.5	5.3		0.23
	Ka‘alaea	8	2.6	2.3	4.3	2.5		−0.1	0.48
	Moku o Lo‘e	2	30.5	20.4	16.0	12.6		**−17.9**	**<0.001**
	Moku o Lo‘e	9	7.7	6.5	6.1	4.1		−3.6	**0.008**
	Pili o Kahe	3	9.0		10.0	10.7	1.7		0.26
	Pūpūkea	4	10.3	13.2		9.6		−0.7	0.76
	Pūpūkea	8	8.3	11.8		8.8	0.5		0.64
Moloka‘i	Kamalō	3		74.6	52.4	55.7		**−18.9**	**<0.001**
	Kamalō	10		75.2	66.1	59.3		**−16.0**	**<0.001**
	Kamiloloa	3		3.7	4.2	2.3		−1.3	**0.03**
	Kamiloloa	10		0.9	2.7	2.7	1.8		**0.007**
	Pālā‘au	3		29.6	26.6	29.0		−0.6	0.87
	Pālā‘au	10		72.4	64.6	72.4		−0.1	0.99
Kaho‘olawe	Hakioawa	3	34.4	32.3	34.0	34.2		−0.2	0.23
	Hakioawa	10	62.0	64.8	63.5	58.4		−3.6	**0.03**
Maui	N. Honolua	3	15.3	17.0	15.1	14.1		−1.1	0.66
	S. Honolua	3	20.9	26.9	23.1	23.9	3.0		**0.01**
	Kahekili	3	43.5		29.4	32.4		**−11.1**	**<0.001**
	Kahekili	7	30.2		21.7	21.1		−8.9	**0.01**
	Kanahena Bay	1	11.3		13.3	11.6	0.2		0.66
	Kanahena Bay	3	21.6		30.0	24.9	3.3		0.16
	Kanahena Pt.	3	3.5		7.2	7.1	3.6		**0.001**
	Kanahena Pt.	10	40.7		33.5	26.9		−13.7	**0.009**
	Mā‘alaea	3	22.0		19.9	18.8		−3.2	0.06
	Mā‘alaea	6	13.4		6.4	5.9		−7.5	**<0.001**
	Molokini	8		64.0	55.9	63.4		−0.6	0.77
	Molokini	13		89.0	77.3	84		−5.0	**0.03**
	Olowalu	3	22.9	24.7	21.5	23.2	0.2		0.72
	Olowalu	7	55.4	54.0	52.6	50.9		−4.5	**0.04**
	Papa‘ula Pt.	4	27.5	31.7	33.2	41.1	**13.6**		**<0.001**
	Papa‘ula Pt.	10	50.3	46.2	43.8	53.4	3.1		**<0.001**
	Puamana	3	14.9	17.7	16.0	13.4		−1.5	0.32
	Puamana	13	2.5	3.1	4.5	6.1	3.6		**<0.001**

TABLE 1 (continued)

Island	Station	Depth (m)	1999	2000	2001	2002	Increase	Decrease[a]	P[b]
Hawai'i	Ka'apuna	4	7.7		10.7		3.0		**0.04**
	Ka'apuna	10	9.8		12.1	15.2	5.4		**0.01**
	Kawaihae	3			21.2	19.6		−1.5	0.42
	Kawaihae	10			32.1	32.5	0.4		0.69
	La'aloa	3		31.6		27.1		−4.5	0.11
	La'aloa	10		40.2		38.6		−1.6	0.41
	Laupāhoehoe	3		11.6		11.1		−0.5	0.58
	Laupāhoehoe	10		10.1		7.2		−2.9	0.41
	Leleiwi	3		12.1		11.6		−0.5	0.78
	Leleiwi	10		31.1		24.5		−6.5	**0.003**
	Nenue Pt.	5	7.6	10.3		12.2	4.5		0.16
	Nenue Pt.	10	15.7	19.1		20.8	5.0		**0.02**

Note: Significant increases or decreases in coral cover are reported using a repeated-measures ANOVA design with contrasts to examine differences between the baseline survey and the last survey.

[a] Decline in coral cover greater than 10% is in **bold** type.

[b] Significant ($P < 0.05$) values are in **bold** type.

TABLE 2

Influential Environmental Parameters and Anthropogenic Factors on Coral Assemblage Characteristics in the Main Hawaiian Islands (Results for the Univariate General Regression Best Subset Models)

	Coral Cover		Species		Diversity	
Parameters	*t* Ratio	P[a]	*t* Ratio	P[a]	*t* Ratio	P[a]
Rugosity	9.9	**<0.001**	2.9	**0.005**	2.2	**0.028**
Depth	2.1	0.037				
Percentage organics			−3.6	**<0.001**	−4.3	**<0.001**
Percentage medium sand					−2.8	**0.005**
Percentage fine sand	2.9	**0.004**			−1.8	0.067
Mean wave height					2.4	**0.016**
Mean wave direction	−3.1	**0.002**	−4.6	**<0.001**	−4.5	**<0.001**
Population within 5 km			−1.6	0.121		
Rainfall	−2.0	**0.044**				
Geologic age	−2.3	**0.023**	−2.8	**0.007**	−2.6	**0.010**

Note: The sign of the *t* ratio indicates the nature of the relationship. Blank cells indicate parameters not suitable in the model.

[a] Significant ($P < 0.05$) values are shown in **bold** type.

Sites in the lower right-hand corner were dominated by the encrusting coral *Montipora flabellata*. These encrusting *M. flabellata* communities were found along north-shore locations that received extreme wave energy, which prohibited development of any coral with vertical relief.

The multivariate BIOENV routine in PRIMER indicated that depth, maximum wave height, rugosity, and percentage organics best explain community structure among all sites. These factors produced the highest matching coefficient (0.38) and accounted for a large portion of the pattern observed in the coral assemblages.

Temporal Trends at the CRAMP Monitoring Sites

Coral cover at most stations changed less than 10% over the 3-yr period (Table 1). A total of 29 out of 60 reefs experienced a sig-

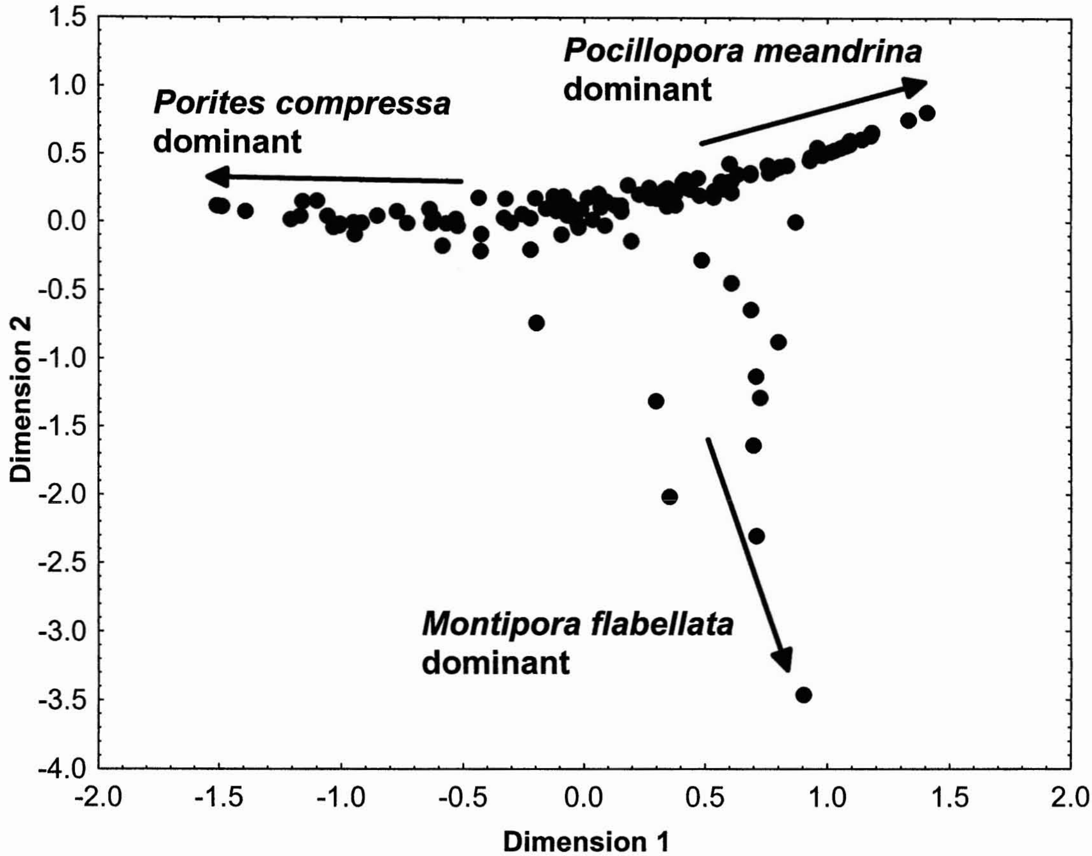

FIGURE 2. Correspondence analysis (CA) results for reef coral community structure for combined monitoring stations and RAT sites ($n = 152$).

nificant change in coral cover from the initial baseline survey to the last survey conducted (Table 1). Sixteen stations showed a significant decline in coral cover, with the greatest drop of 19% occurring at the Kamalō 3-m station on Moloka'i. In contrast, 13 stations increased in coral cover, with the greatest increase of 14% at the Papa'ula Point 4-m station on Maui. There is one problematical site (2-m station at Ka'alaea, O'ahu), which showed high fluctuations between samplings. This appeared to be caused by one or more major slumping events involving large sections of reef. Some of the marking pins and blocks of live coral between the pins were moved by the slumping. Continued monitoring should resolve this question.

Figures 3–4 provide a spatial representation of significant declines or increases in coral cover at each station by depth. Changes of <10% in coral cover may be significant but may not be biologically relevant over the long run due to natural cycles inherent in coral communities and possible measurement and observer error. In general, a time scale of decades is needed to assess long-term trends on coral reefs. Consequently, temporal trends should be interpreted with caution over the relatively short time span of the study. This study did identify six reefs (10% of the total) that had major shifts in coral cover >10%, which warrant further experimental investigation and more detailed observations in the future.

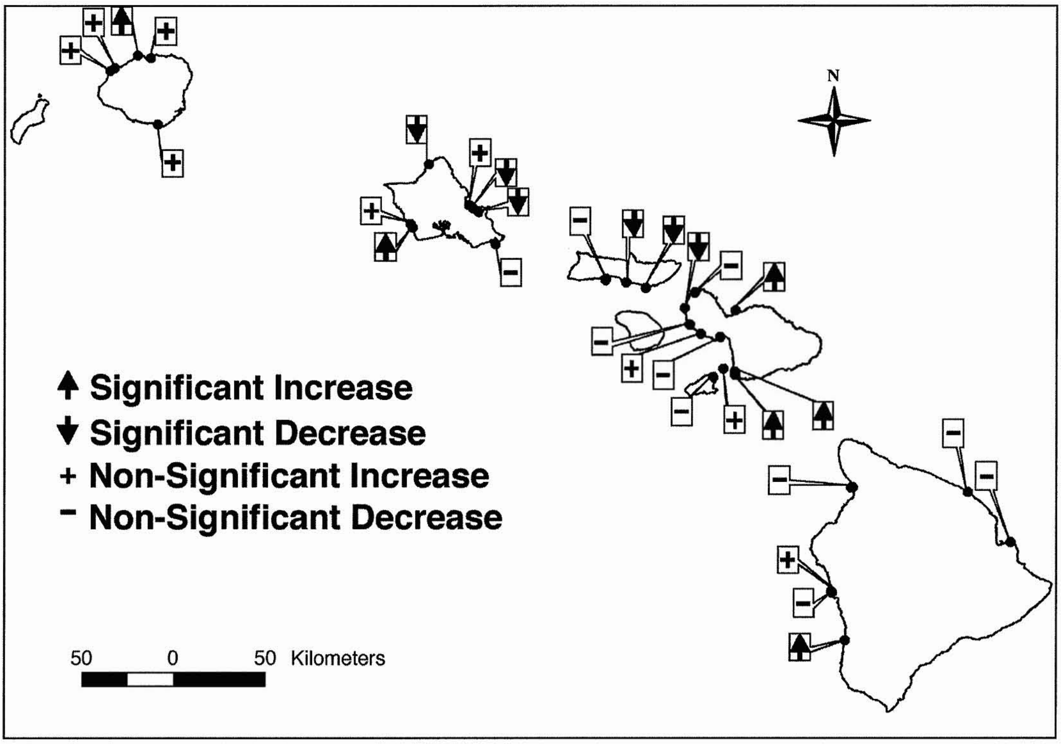

FIGURE 3. Changes in coral cover at each of the shallow (<5 m) monitoring sites.

Change and factors related to change were revealed by the results of the Best Subset GLM. Percentage change in coral cover was significant ($R_a^2 = 0.39$; $F = 8.6$; df $= 5{,}54$; $P < 0.001$) among stations. Rugosity ($F = 23.2$; df $= 1{,}54$; $P < 0.001$), mean wave height ($F = 5.0$; df $= 1{,}54$; $P = 0.030$), and area of the adjacent watershed ($F = 4.7$; df $= 1{,}54$; $P = 0.035$) accounted for a significant portion of the variation in percentage change in coral cover (Table 3). Percentage organics ($F = 3.3$; df $= 1{,}54$; $P = 0.075$) and minimum wave height ($F = 3.5$; df $= 1{,}54$; $P = 0.068$) were marginally nonsignificant predictor variables in the model. A positive relationship existed between percentage change in coral cover and mean wave height, minimum wave height, and watershed area. Percentage change in coral cover, however, had a negative relationship with rugosity and percentage organics.

DISCUSSION

The monitoring and assessment program developed by CRAMP from 1998 to 2002 represents the first systematic and broadly comprehensive description of the spatial differences and the temporal changes in Hawaiian reef coral communities and will provide the basis for determining the future long-term (decadal) trends on Hawaiian coral reefs. Results will become statistically more powerful with repeated measurement over time. Information collected to date provides insights into ecological factors controlling reef coral community structure and reef coral community dynamics. These data allow testing of ecological hypotheses and serve as a tool for resource management decisions. For example, the initial CRAMP fish and benthic data have been used to describe the influence of habitat, fishing pressure, and Marine

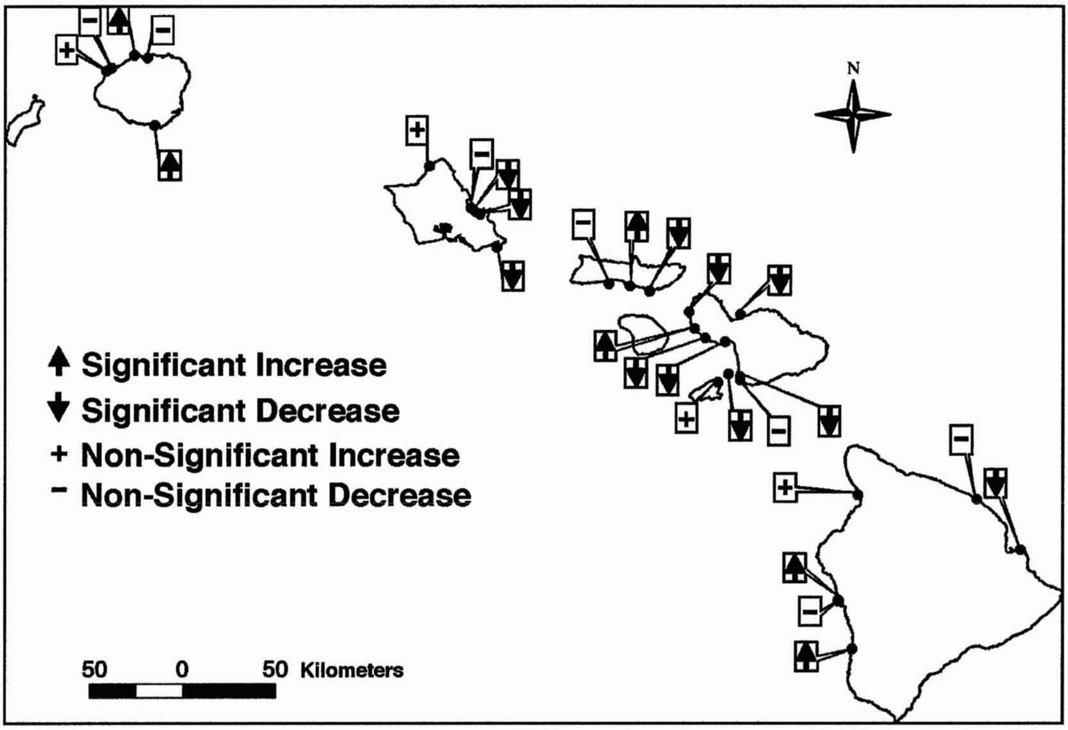

FIGURE 4. Changes in coral cover at each of the deep (>5 m) monitoring sites.

TABLE 3

Influential Environmental Parameters and Anthropogenic Factors on Temporal Trends in Coral Cover in the Main Hawaiian Islands (Results for the Univariate General Regression Best Subset Models)

	% Change in Coral Cover	
Parameters	*t* Ratio[a]	P^b
Rugosity	−4.8	**<0.001**
% Organics	−1.8	0.075
Mean wave height	2.2	**0.030**
Minimum wave height	1.9	0.068
Watershed area	2.2	**0.035**

[a] The sign of the *t* ratio indicates the nature of the relationship.
[b] Significant ($P < 0.05$) values are shown in **bold** type.

Protected Areas on reef fish community structure (Friedlander and DeMartini 2002, Friedlander et al. 2003).

The results of the univariate analysis shown in Table 2 illustrate the dilemma of the coral reef ecologist. Numerous significant factors influence various biological parameters, so the situation is complex and no single environmental variable can be used to predict the coral community characteristics. Univariate analysis of the spatial data set revealed that various biological parameters (i.e., coral cover, coral species richness, and coral diversity) show a significant relationship with the physical factors of rugosity, sediment composition, mean wave direction, mean wave height, rainfall, and geologic age of the Islands. The multivariate BIOENV analysis links the multivariate biological variable to the environmental parameters and identified four parameters (maximum wave height, geologic age, rugosity, and percentage of silt) that are the most important in explaining variation in coral community structure. These observations are consistent with and amplify the findings of many previous classic studies:

(1) Maximum wave height is an index of storm wave damage to reefs. Dollar (1982) and Storlazzi et al. (2002) showed that waves in Hawai'i can reach destructive levels that will damage corals and restrict species distribution patterns. The univariate analysis (Table 2) also showed that mean wave direction (expressed as compass bearing) showed a negative relationship with coral cover, species richness, and diversity. This is because major storm surf in Hawai'i (Figure 1) arrives along a gradient that roughly diminishes in a counterclockwise direction from the north (Moberly and Chamberlain 1964). The result is a positive correlation between wave direction and wave height. The largest and most frequent storm surf arrives during the winter North Pacific Swell (bearing 315°), with the less frequent and less damaging storm waves during the summer from the South Swell (bearing 190°) to the less severe Trade Wind Swell (bearing 45°) (Figure 1). Sites exposed to west and northwest swells on the older islands (e.g., Kaua'i and O'ahu) generally had lower coral coverage, species richness, and diversity.

(2) Geologic age is a major factor influencing reef coral community structure as indicated by both the univariate and multivariate analysis. The Hawaiian Islands formed over the hot spot located near the southeastern end of the archipelago and over millions of years have gradually moved to the northwest on the Pacific Plate. The Islands are thus moving to higher latitude over time, so there is a high correlation (0.95) between island age and latitude. Light and temperature conditions favorable to coral growth diminish with increasing latitude and increasing island age. Grigg (1982) previously demonstrated that coral growth and coral cover diminishes with latititude (= age) along the Hawaiian Archipelago over the range from the island of Hawai'i (19 °N) to Kure Atoll (28.5 °N). Our study was conducted over a smaller latitudinal range (19 °N to 22 °N) but with a much more extensive sample and shows the importance of island age or latitude on reef coral community structure within the main Hawaiian Islands.

(3) Rugosity was shown to be an important factor by both the univariate and multivariate analyses. Areas of antecedent high rugosity allow corals to attach and grow on higher substrata not influenced by sand and sediment movement along the bottom. Birkeland et al. (1981) and Rogers et al. (1984) observed that coral larvae preferentially recruited to vertical surfaces and suggested that this pattern also applied to areas of higher rugosity. As coral reef communities develop, the structure and continued accretion of the coral skeletons further increase rugosity. Thus both physical and biological components are involved in development of high-rugosity environments.

(4) Sediment components played a role in explaining variation in the coral assemblage characteristics. Percentage organics, an indicator of terrigenous input, showed negative relationships with coral species richness and diversity. Higher percentage organic content was also important in explaining decline in coral cover over time in the temporal analysis of the monitoring site data. Other studies have determined that increased terrigenous input has an adverse impact on reef communities (Acevedo and Morelock 1988, Rogers 1990, van Katwijk et al. 1993).

The importance of wave energy in shaping Hawaiian coral communities can be clearly seen in the results of the correspondence analysis (Figure 2), with all of the sites falling along a gradient. Shallow high-wave-energy communities dominated by the coral *Pocillopora meandrina* grade through *Porites lobata*–dominated communities to deeper low-water-motion *Porites compressa*–dominated communities. Another axis controlled by extremely high water motion and the encrusting coral *Montipora flabellata* is also present. This pattern is consistent with results of other studies of wave energy in relation to reef coral zonation (Grigg and Maragos 1974, Dollar 1982). The relationship between coral community structure and sediment grain size distribution is also determined to a large extent by wave energy, currents, and bathymetry (Gagan et al. 1988). Waves sort the coarser sediments, accelerate currents, and transport the finer sediment fractions offshore into deeper water. High-wave-exposure

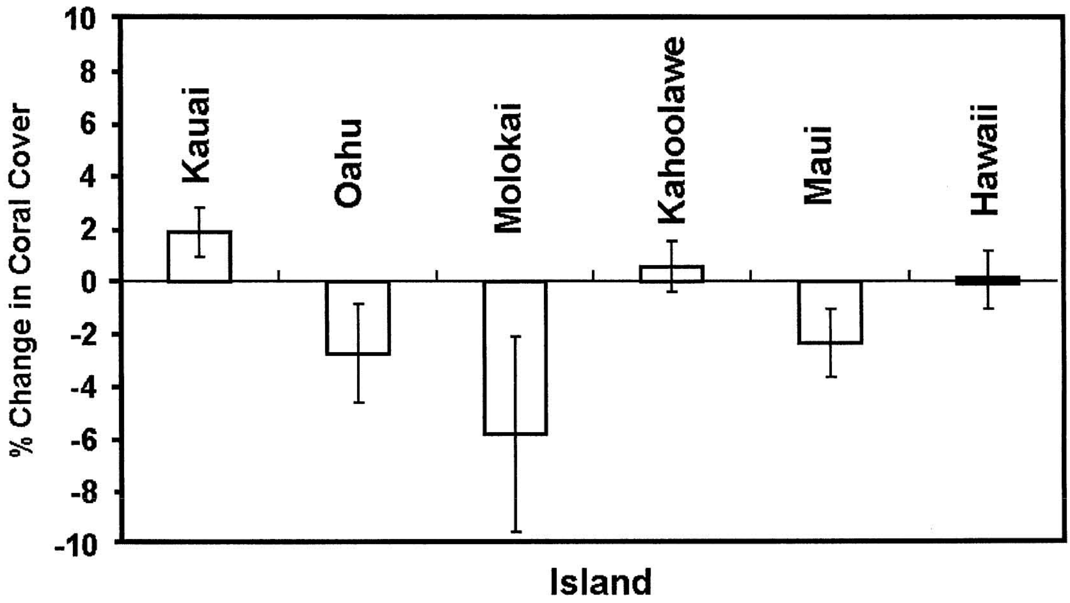

FIGURE 5. Mean percentage change ± SE in coral cover by island from 1999 to 2002.

sites generally have coarser grain size distributions.

Patterns of change in coral cover measured in this study are consistent with observations of other studies in Hawai'i. For example, coral coverage has declined at monitoring sites in Kāne'ohe Bay in the past 3 yr, which is a continuation of a trend noted in the bay over the previous 20 yr (Hunter and Evans 1993, Evans 1995, Stimson et al. 2001). Along the south shore of Moloka'i a large zone of damaged reef occurs in the middle portion of the coastline at Kamiloloa. This location has the lowest coral coverage of all monitoring stations in the state, but is located midway between two other South Moloka'i locations (Pālā'au and Kamalō) that have very high coverage. This anomaly can be explained by increases in nearshore sedimentation due to historical overgrazing and poor land management practices (Roberts 2001). In addition, the construction of the Kaunakakai causeway appears to have played a role in blocking long-shore currents, thereby reducing the rate of sediment and nutrient removal. In contrast, an increase in coral was measured at Limahuli, Kaua'i, where the watershed is being effectively managed in a near-pristine state.

The downward trend of average coral coverage on Hawaiian reefs as measured in this study appears to be most prevalent in the central portion of the archipelago on the islands of O'ahu, Moloka'i, and Maui (Figure 5). Most of the human population of Hawai'i resides on O'ahu (72%) and Maui (10%). Moloka'i has a lower human population but suffers from extreme erosion and sedimentation of reefs along the south shore due to inadequate watershed management (Roberts 2001). Maui also suffers from impaired watersheds and population centers that are adjacent to major reef areas (West Maui Watershed Management Advisory Committee 1997). The islands of Kaua'i and Hawai'i have relatively low human population and show an increase in coral reef coverage. At Kaho'olawe, a former military target island, the condition of sediment-impacted reefs has held steady following the removal of all grazing animals, cessation of bombing, and a massive program of revegetation.

Turgeon et al. (2002:53) reported, "the consensus of many ecologists is that, with a few exceptions, the health of the near-shore reefs around the Main Hawaiian Islands remains relatively good." On the other hand, some researchers, local fishermen, and recreational divers with long-term experience observe that reefs in many areas of Hawai'i have declined over past decades. For example, Jokiel and Cox (1996) noted degradation of Hawaiian reefs due to human population growth, urbanization, and coastal development. Absence of the catastrophic short-term reef declines that have been noted in other geographic areas (e.g., Hughes 1994) can lead to the impression that Hawaiian reefs are in good condition. However, slow rates of decline will eventually result in severely degraded reefs. This decline will go undetected by researchers and managers without rigorous monitoring over a wide spatial array at time intervals measured in decades. The spatial patterns and temporal change of reef coral community structure in relation to human population that were observed in this study suggest that the rapidly growing human population of Hawai'i may be having an effect on the reefs. The observed decline of many coral reefs in Hawai'i over the short term is a cause for concern. A longer time series is needed because coral reefs can undergo natural oscillations with a period of decades (Done 1992). However, the declines observed to date in Hawai'i are mainly associated with areas of high human population or impaired watersheds, suggesting anthropogenic rather than natural causes.

In general, reefs recover from acute disturbances but not from situations where gradual declines led to their demise (Connell et al. 1997). Slow declines in condition of reefs that are associated with areas of high human population suggest broad anthropogenic alterations of the physical and biological environment. Decline can be due to a combination of factors such as sedimentation (Acevedo and Morelock 1988), eutrophication (Bell and Elmetri 1995), overexploitation of fisheries resources (Hughes 1994), coastal construction, damage due to toxic materials (Pastorok and Bilyard 1985), and introduction of exotic species. In Hawai'i, time will tell if the current rate of decline signals a demise or phase shift from reefs dominated by corals to reefs abundant with macroalgae and other organisms.

Coral decline appeared to be greater at the deeper sites compared with the shallow sites (Figures 3–4). Connell et al. (1997) noted that the space and time scales of declines and recoveries in coral abundance were much smaller on the wave-exposed side of a reef than on the side protected from storms. Perhaps this concept can be extended to include the vertical gradient in wave energy. The more robust nature of the shallow reefs and higher flushing due to greater wave action may allow these coral communities to tolerate perturbations (Jokiel 1978).

In sum, it is clear from the results of this study that there are no simple answers to complex ecological questions. The broad approach taken in this study has shown the importance of major factors such as wave energy, island age, rugosity, and sediment composition on coral reef community structure. The study has identified a number of sites and areas of special environmental concern that will be monitored and described in more detail. An extensive baseline has been established that has characterized a broad cross section of Hawaiian coral reef habitats and will eventually allow description of long-term changes due to both natural and anthropomorphic factors. Understanding how natural forces shape our coral reefs is a prerequisite to understanding the role of human impact on these ecosystems. Above all, we must be able to detect long-term changes on reefs if we are to identify problems, develop possible solutions, and evaluate the effectiveness of such management action.

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